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Response to selection and changes in genetic parameters for 13 plant and ear traits in two maize recurrent selection programs

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Abstract
Recurrent selection is a cyclical breeding procedure that focuses on improving the mean performance of a population by increasing the frequency of favorable alleles and maintaining adequate genetic variability for continued selection response. The Iowa Stiff Stalk Synthetic (BSSS) maize (Zea mavs L.) population has undergone continuous recurrent selection for more than 50 years as the base population for two independent selection programs. This study was designed to estimate the mean performance and important genetic parameters in BSSS before and after seven cycles of half- sib (I IS) progeny selection, six cycles of Srprogeny selection, and 11 cycles of reciprocal recurrent selection (RRS). A Design II (factorial) mating design was constructed to give direct estimates of additive and dominance variance in the individual populations. Progenies from each of the four populations were grown for two years in a randomized incomplete block experiment. The relative effectiveness of the three selection methods for improving the mean performance: for grain yield of the BSSS populations per se was 0.4'Vi1 cycle-1 for HS selection, 1.1% cycle-1 for Srprogeny selection, and 1.4% cycle- 1 for RRS. There were few changes in variance components after selection for most of the traits. Additive variance generally accounted for the largest portion of the total genetic variance for all traits except grain yield The importance of dominance variance for grain yield implied that interpopulation and testcross selection methods may give the greatest direct response to selection. The estimates of heritability and corresponding estimates of additive genetic variance indicated that continued response to selection is expected for each selection method. Selection pressure on the primary agronomic traits did not seem to affect the mean performance and genetic parameters of the other unselected agronomic traits.

Keywords
Corn, Recurrent selection, Selection progress, Additive variance, Dominance variance

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RESPONSE TO SELECTION AND CHANGES IN GENETIC PARAMETERS FOR 13 PLANT AND EAR TRAITS IN TWO MAIZE RECURRENT SELECTION PROGRAMS[1]

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ABSTRACT - Recurrent selection is a cyclical breeding procedure that focuses on improving the mean performance of a population by increasing the frequency of favorable alleles and maintaining adequate genetic variability for continued selection response. The Iowa Stiff Stalk Synthetic (BSSS) maize (*Zea mays* L.) population has undergone continuous recurrent selection for more than 50 years as the base population for two independent selection programs. This study was designed to estimate the mean performance and important genetic parameters in BSSS before and after seven cycles of half-sib (HS) progeny selection, six cycles of S_2-progeny selection, and 11 cycles of reciprocal recurrent selection (RRS). A Design II (factorial) mating design was constructed to give direct estimates of additive and dominance variance in the individual populations. Progenies from each of the four populations were grown for two years in a randomized incomplete block experiment. The relative effectiveness of the three selection methods for improving the mean performance for grain yield of the BSSS populations per se was 0.4% cycle^{-1} for HS selection, 1.1% cycle^{-1} for S_2-progeny selection, and 1.4% cycle^{-1} for RRS. There were few changes in variance components after selection for most of the traits. Additive variance generally accounted for the largest portion of the total genetic variance for all traits except grain yield The importance of dominance variance for grain yield implied that interpopulation and testcross selection methods may give the greatest direct response to selection. The estimates of heritability and corresponding estimates of additive genetic variance indicated that continued response to selection is expected for each selection method. Selection pressure on the primary agronomic traits did not seem to affect the mean performance and genetic parameters of the other unselected agronomic traits.

KEY WORDS: Corn; Recurrent selection; Selection progress; Additive variance; Dominance variance.

INTRODUCTION

Recurrent selection is a cyclical breeding procedure used widely in maize (*Zea mays* L.) breeding programs to enhance maize germplasm resources. Population improvement via recurrent selection methodology focuses on two main objectives: improving the mean performance of a population by increasing the frequency of favorable alleles and maintaining adequate genetic variability in the improved population for continued selection and genetic enhancement. By increasing the frequency of favorable alleles, recurrent selection increases the probability of developing inbred lines with superior combining ability.

The Iowa Stiff Stalk Synthetic (BSSS) maize population was developed in the mid-1930s by intermating 16 inbred lines with above-average stalk quality (SPRAGUE, 1946). Since its development, BSSS has undergone continuous recurrent selection for more than 50 years as the base population in two independent selection programs. The first program included seven cycles of half-sib (HS) selection with the double-cross tester Iowa 13 [BSSS(HT)Cn], followed by six cycles of S_2-progeny selection [BS13(S)Cn], which continues to date. The second program included 11 cycles of reciprocal recurrent selection (RRS) using BSSS, designated BSSS(R)Cn, and Iowa Corn Borer Synthetic #1 [BSCB1(R)Cn] as base populations undergoing simultaneous improvement. As a consequence of these selection programs, BSSS has contributed significantly to maize inbred and hybrid development programs, as evidenced by the development of several widely-used inbred lines (B14, B37, B73, and B84) (HALLAUER *et al.*, 1983).

HOLTHAUS and LAMKEY (1995) reported on the effects of selection on the population means and genetic variances for the traits of machine harvestable grain yield, grain moisture at harvest, root lodging, and stalk lodging. These traits were of primary interest because they

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had been used as selection criteria. Also of interest is determining the effect of selection on the population means and genetic variances for correlated plant and ear traits that could not be measured in machine-harvested plots. We estimated the population means and genetic variances for hand-harvested grain yield, root and stalk lodging, pollen shed, silk emergence, plant and ear height, number of ears plant^{-1}, kernel row number, ear length and diameter, kernel depth, and 300-kernel weight for BSSSC0, BS13(S)C0, BS13(S)C6, and BSSS(R)C11. The objective was to determine if selection had changed the population parameters.

MATERIALS AND METHODS

Genetic Materials Evaluated

In 1939, HS progeny recurrent selection using the double-cross tester Iowa 13 [(L317 x BL349) x (BL345 x MC410)] was initiated in BSSSC0. The procedures for conducting seven cycles of HS selection in this population were described by Eberhart *et al.* (1973) and Lamkey *et al.* (1991). After seven cycles of selection, the program was changed to S_2-progeny recurrent selection in the population now designated BS13(S)C0. BS13(S)C0 was developed directly from the seventh cycle population of the HS program by imposing minor agronomic selection as detailed by Lamkey (1992). Six cycles of S_2-progeny selection were completed, as summarized by Helms *et al.* (1989) and Lamkey (1992), producing the advanced cycle population BS13(S)C6.

In 1949, RRS was initiated in the BSSS and BSCB1 maize populations. The base population, BSSSC0, used in this program is identical to the original BSSS population used in the HS selection program. Details of 11 cycles of this interpopulation selection program were outlined by Penney and Eberhart (1971) and Keeratinijakal and Lamkey (1993). The Cycle 11 (C11) population of BSSS was designated BSSS(R)C11.

In all three selection programs, grain yield was the primary trait under selection, with secondary selection pressure to maintain low grain moisture at harvest and increase resistance to root and stalk lodging. Beginning with C9 of RRS and C3 of S_2-progeny selection, progenies were selected by using a selection index weighted by the heritabilities of grain yield, grain moisture, root lodging, and stalk lodging. The selection intensities averaged 9.7% for HS selection, 15.6% for S_2-progeny selection, and 12.1% for RRS. The harmonic mean of the number of progenies recombined in each selection program is 10 for HS selection, 15 for S_2-progeny selection, and 11.6 for RRS. Assuming an effective population size of 2N, where N is the number of progenies recombined, the estimated inbreeding level of the four populations due to small effective population size is 0% for BSSSC0, 29% for BS13(S)C0, 45% for BS13(S)C6, and 37% for BSSS(R)C11 (Keeratinijakal and Lamkey, 1993; Lamkey, 1992).

The genetic materials evaluated in our study were produced from BSSSC0 and three populations derived from BSSSC0 by selection: BS13(S)C0, BS13(S)C6, BSSS(R)C11. Starting in the 1989 breeding nursery, a North Carolina Design II (factorial) mating design was developed within each of the four populations. A series of half- and full-sib progenies was developed within each population by crossing four males (S_0 plants) to each of four females (S_1 progenies). S_1 progenies were developed in the 1988 breeding nursery by selfing random S_0 plants from each population. Each male was crossed to several plants within a S_1 progeny, and the resulting seed was bulked to obtain a representative sample of the gametic array of the original S_0 female plant (Hallauer and Miranda, 1988). The average number, variance, and range of S_1 plants sampled per female within each population were: 9, 11.1, and 1 to 19 for BSSSC0; 9, 8.4, and 4 to 19 for BS13(S)C0; 13, 7.8, and 4 to 20 for BS13(S)C6; and 13, 7.5, and 5 to 20 for BSSS(R)C11. Thus, each set of four x four matings produced progenies from a sampling of eight random plants within each population. To achieve a reasonable sample of individuals, 14 sets of four x four matings were constructed within each population, yielding a total sampling of 112 random S_0 plants from each population. Therefore, 224 full-sib progenies (14 sets of 16 progenies) from each population were produced for field evaluation.

Experimental Design and Procedures

The 896 entries (full-sib progenies) were evaluated in 14 sets of a replications-within-sets randomized incomplete block experiment (Comstock and Robinson, 1948). Because of insufficient seed supply, eight entries were replaced with hybrid filler in all years. Each set included 16 full-sib progenies from each of the four individual populations completely randomized within each of two replications. The study was grown at Ames, IA, in 1992 and 1993. One of the 14 sets was discarded in 1993 because of damage from standing water. Therefore only 13 sets were analyzed from 1992 and 1993, whereas, Holthaus and Lamkey (1995) analyzed 14 sets. A plot consisted of one row 5.49 m long with 0.76 m between plots. Plots were overplanted and thinned to a uniform plant density of approximately 62,165 plants ha^{-1}. All experiments were machine-cultivated and/or hand weeded as necessary.

Data were collected for hand-harvested grain yield (Mg ha^{-1}) including gleaning for dropped ears, stand (plants ha^{-1}), root lodging (percentage of plants leaning more than 30° from vertical), stalk lodging (percentage of plants broken at or below the primary ear node), pollen shed measured as growing degree units in °C (GDU °C), silk emergence (GDU °C), plant and ear height (cm), number of ears plant^{-1} (total number of ears harvested divided by final plant stand), kernel row number (average of 10 random primary ears), ear length and diameter (cm), cob diameter (cm), kernel depth (cm), and 300-kernel weight (g). Plant and ear heights were calculated as the average measurement of 10 competitive plants per plot, measured as the distance from the soil surface to the flag leaf node and highest ear-bearing node, respectively. Pollen shed and silk emergence were measured as accumulated growing degree units (GDU) in °C from planting until 50% of the plants in the plot had shed pollen and emerged silks, respectively. Growing degree units were calculated as the daily maximum plus minimum temperature divided by two, minus 10°C (Shaw, 1988). Any maximum temperature greater than 30°C or minimum temperature less than 10°C was designated in the equation as the appropriate base temperature of 30°C or 10°C, respectively. Ear length and diameter, and cob diameter were measured as the average of 10 random primary ears. Kernel depth was calculated as ear diameter minus cob diameter, divided by two. All traits were measured in each year. Because uniform plant stands were not achieved, grain yield data were adjusted for plant population by using covariance analysis.

Statistical Methods

Analyses for all traits were calculated on the basis of plot mean data. The data for each trait were analyzed by pooling over sets and combining across years in the general analyses, with all effects in the model considered random. The sums of squares for among en-

tries, among entries by years, and pooled error were partitioned into sources of variation due to among and within populations. Because of the missing entries, within-population degrees of freedom were adjusted appropriately. The variance of a population mean was calculated as the mean square for genotypes within sets for the appropriate population divided by the total number of observations in the mean. The among population sums of squares were then further partitioned into three contrasts (one non-orthogonal and two orthogonal) to compare the effect of seven cycles of HS progeny selection [BSSSC0 vs. BS13(S)C0], six cycles of S_2-progeny selection [BS13(S)C0 vs. BS13(S)C6], and 11 cycles of RRS [BSSSC0 vs. BSSS(R)C11]. Contrast mean squares were tested for significance using the corresponding interaction with years mean squares.

Analyses for individual populations pooled over sets and combined across years were calculated to partition the within-population variation for each population into male, female, and male x female interaction sources of variation. Because the missing entries caused some of the four by four sets to be unbalanced, the appropriate male or female was deleted yielding some three by four balanced sets. Because the mean squares for the male and female sources of variation have the same genetic expectation, their degrees of freedom and sums of squares were pooled to give more precise estimates of the variation among half-sib families. The within-population by year interaction degrees of freedom and sums of squares were partitioned similarly. Within-population error mean squares were used to test the significance of the within-population by year interaction sources of variation. The appropriate interaction mean squares were then used for testing the within-population components. Since direct tests of the male, female, and pooled components were not available, SATTERTHWAITE'S (1946) approximation was used to construct the appropriate F-test.

Covariances of relatives, estimated from the analysis of variance, were translated into appropriate genetic components of variance given that the inbreeding coefficient (F) of the parents was zero (COMSTOCK and ROBINSON, 1948). Additive genetic ($\hat{\sigma}^2_A$), dominance genetic ($\hat{\sigma}^2_D$), additive x year ($\hat{\sigma}^2_{AY}$), dominance x year ($\hat{\sigma}^2_{DY}$), and error ($\hat{\sigma}^2_E$) variance components were calculated by equating the observed mean squares to the expected mean squares and solving the resulting system of equations. Additive and additive x year variance components were calculated by using the male and female pooled and its interaction with years mean squares, respectively. Approximate 90% confidence intervals were calculated for each variance component estimate according to the procedures of BURDICK and GRAYBILL (1992). Variance components were declared significantly different from zero if the approximate 90% confidence interval did not bracket zero. Comparisons of variance components between populations were declared significant if their confidence intervals did not overlap. Negative estimates of variance components were reported as such. These estimates were not significantly different from zero. Heritabilities and their exact 90% confidence intervals (KNAPP and BRIDGES, 1987) were estimated on a half-sib progeny mean basis for individual traits within each population. Phenotypic and additive genetic correlations among traits within populations were calculated from the appropriate covariance components (MODE and ROBINSON, 1959).

RESULTS AND DISCUSSION

The average grain yield was 5.22 Mg ha^{-1} and ranged from 7.04 Mg ha^{-1} in 1992 to 3.39 Mg ha^{-1} in 1993. Pollen shed and silk emergence averaged 841 and 854 GDU (°C), respectively. Because of excessive rainfall and below average temperatures during the 1993 growing season, grain yield was approximately 50% of the 1992 average and anthesis was 7.0% later. Root and stalk lodging averaged 2.9 and 10.8%, respectively. Plant and ear heights averaged 224 and 112 cm, respectively, and ears plant^{-1} averaged 0.93. Ear length and diameter averaged 15.0 and 4.4 cm, respectively, and mean kernel row number was 16.3. Average kernel depth was 0.76 cm, and the mean weight of a 300-kernel sample was 60.0 g. The poor growing conditions experienced during 1993 increased the number of barren plants and adversely affected most of the ear and kernel traits. However, coefficients of variation for all traits in both years were generally small, indicating that adequate precision was maintained during data collection. There were no indications that the 1993 data should have been deleted from the analysis.

Effects of Selection on Population Mean Performance

Measurement of the average linear response to selection of the various traits was based on population per se performance. Therefore, changes measured in HS and RRS programs are indirect responses to selection, whereas those measured in S_2-progeny selection programs are direct responses to selection.

Half-sib Progeny Selection

Half-sib progeny selection was ineffective for improving the mean grain yield in BSSS. Seven cycles of HS progeny selection resulted in a nonsignificant indirect response to selection of 0.15 Mg ha^{-1} or 0.4% cycle^{-1} (Table 1). This response to selection was significantly less than the response of 1.9% cycle^{-1} observed by HOLTHAUS and LAMKEY (1995). Differences among studies in the average linear rate of response may be a function of the number of environments in which the materials were evaluated and/or differences in methods of evaluation and data collection. Grain yield data in our study were measured from hand-harvested, single-row plots grown at one location in each of two years, whereas, the data of HOLTHAUS and LAMKEY (1995) were based on machine-harvested, two-row plots grown in six environments. Full-sib progeny frequency distributions for grain yield showed that seven cycles of HS selection [BSSSC0 vs. BS13(S)C0] were only effective for eliminating the extreme phenotypes from the distribution, resulting in a 41% reduction in phenotypic variation (Fig. 1). Responses to HS progeny selection for the

TABLE 1 - *Means, error variances, and coefficients of variation from the combined analysis of variance over 1992 and 1993 for 13 traits measured in four BSSS populations.*

Trait	Mean ± SE	$\hat{\sigma}^2_c$	CV (%)	Trait	Mean ± SE	$\hat{\sigma}^2_c$	CV (%)
Grain yield (Mg ha^{-1})				Ears plant^{-1} (no.)			
BSSSC0	4.85 ± 0.05	0.581	15.7	BSSSC0	0.84 ± 0.006	0.009	11.3
BS13(S)C0	5.00 ± 0.04	0.314	11.2	BS13(S)C0	0.95 ± 0.005	0.011	11.0
BS13(S)C6	5.37 ± 0.04	0.356	11.1	BS13(S)C6	0.96 ± 0.006	0.010	10.4
BSSS(R)C11	5.62 ± 0.04	0.261	9.1	BSSS(R)C11	0.98 ± 0.004	0.005	7.2
Root lodging (%)				Kernel row number (no.)			
BSSSC0	2.5 ± 0.2	26.05	204.2	BSSSC0	16.7 ± 0.07	0.52	4.3
BS13(S)C0	5.0 ± 0.4	50.64	142.3	BS13(S)C0	15.6 ± 0.05	0.46	4.3
BS13(S)C6	3.4 ± 0.3	49.41	206.7	BS13(S)C6	15.1 ± 0.05	0.31	3.7
BSSS(R)C11	0.6 ± 0.1	6.82	435.3	BSSS(R)C11	17.9 ± 0.06	0.40	3.5
Stalk lodging (%)				Ear length (cm)			
BSSSC0	14.0 ± 0.4	59.91	55.3	BSSSC0	15.0 ± 0.06	0.814	6.0
BS13(S)C0	9.3 ± 0.4	51.32	77.0	BS13(S)C0	14.9 ± 0.05	0.813	6.1
BS13(S)C6	11.2 ± 0.3	47.50	61.5	BS13(S)C6	15.6 ± 0.05	0.609	5.0
BSSS(R)C11	8.6 ± 0.3	41.33	74.8	BSSS(R)C11	14.6 ± 0.05	0.496	4.8
Pollen shed (GDU °C)				Ear diameter (cm)			
BSSSC0	846 ± 1.0	102.2	1.2	BSSSC0	4.4 ± 0.01	0.048	5.0
BS13(S)C0	844 ± 0.8	113.3	1.3	BS13(S)C0	4.4 ± 0.01	0.079	6.4
BS13(S)C6	852 ± 0.8	89.2	1.1	BS13(S)C6	4.3 ± 0.01	0.098	7.3
BSSS(R)C11	822 ± 0.9	88.3	1.1	BSSS(R)C11	4.4 ± 0.01	0.009	2.2
Silk emergence (GDU °C)				Kernel depth (cm)			
BSSSC0	867 ± 1.1	153.6	1.4	BSSSC0	0.81 ± 0.005	0.011	12.9
BS13(S)C0	858 ± 0.8	126.4	1.3	BS13(S)C0	0.75 ± 0.006	0.019	18.4
BS13(S)C6	861 ± 0.9	115.5	1.2	BS13(S)C6	0.68 ± 0.006	0.026	23.7
BSSS(R)C11	829 ± 1.1	149.8	1.5	BSSS(R)C11	0.81 ± 0.003	0.004	7.8
Plant height (cm)				300-kernel weight (g)			
BSSSC0	230 ± 0.5	37.6	2.7	BSSSC0	58.8 ± 0.35	29.10	9.2
BS13(S)C0	224 ± 0.5	39.1	2.8	BS13(S)C0	61.2 ± 0.35	33.16	9.4
BS13(S)C6	220 ± 0.5	32.3	2.6	BS13(S)C6	60.0 ± 0.33	20.51	7.5
BSSS(R)C11	221 ± 0.5	37.0	2.8	BSSS(R)C11	58.1 ± 0.29	18.41	7.4
Ear height (cm)							
BSSSC0	121 ± 0.5	35.2	4.9				
BS13(S)C0	115 ± 0.5	25.7	4.4				
BS13(S)C6	110 ± 0.5	29.3	4.9				
BSSS(R)C11	100 ± 0.5	36.4	6.0				

agronomic traits undergoing secondary selection pressure were generally favorable and consistent with results reported by HOLTHAUS and LAMKEY (1995). Grain moisture at harvest was not measured, but significant decreases in GDU (°C) to pollen shed and silk emergence means suggest a tendency toward earlier maturing genotypes. Stalk lodging was reduced significantly (0.7% cycle^{-1}) with HS selection. Root lodging, however, increased slightly (0.4% cycle^{-1}) as a consequence of the positive selection differential (LAMKEY, 1992).

The responses of other plant and ear traits to HS selection were generally in a favorable direction, even though no direct selection pressure was applied to them. Average plant and ear height decreased significantly (0.9 and 1.0 cm cycle^{-1}, respectively) with HS selection. HOLTHAUS and LAMKEY (1995) reported an identical decrease in mean ear height and STUCKER and HALLAUER (1992) reported a tendency toward reduced plant and ear height in random S_7 lines developed from the BSSS after HS selection. The number of ears plant^{-1} increased significantly (0.11), accompanied by

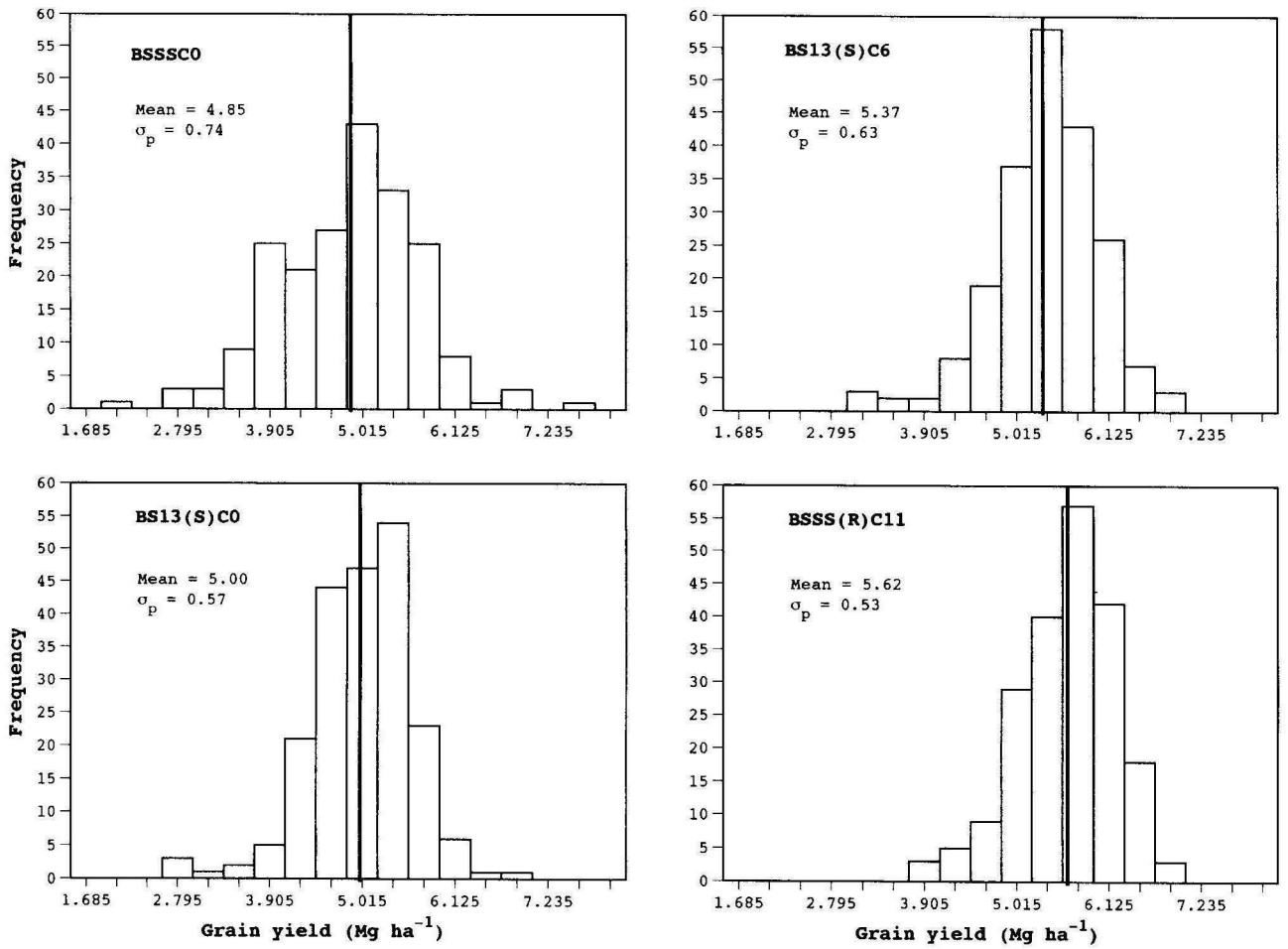

FIGURE 1 - Frequency distribution, mean, and phenotypic standard deviation for grain yield of full-sib progenies from BSSSC0, BS13(S)C0, BS13(S)C6, and BSSS(R)C11 maize populations. Distances between class intervals are one half of a phenotypic standard deviation of the BSSSC0 population. Vertical lines represent the population means.

a significant decrease in the number of kernel rows per ear (1.1). Although statistically significant decreases in ear length and kernel depth were observed, the changes were not agronomically important. HS selection produced no change in the mean ear diameter. Similar results for ear length and diameter were reported by STUCKER and HALLAUER (1992). The relatively large increase in 300-kernel weight (2.4 g) after seven cycles of HS selection was not statistically significant because of a large genotype by year interaction.

S_2 Progeny Selection

The average linear direct response to selection for grain yield after six cycles of S_2-progeny selection was significant (0.37 Mg ha^{-1} or 1.1% cycle^{-1}, Table 1). This result was in good agreement with the 1.2% cycle^{-1} response observed by HOLTHAUS and LAMKEY (1995). Six cycles of S_2-progeny selection [BS13(S)C0 vs. BS13(S)C6] were effective in increasing the mean performance of the population and maintaining the original level of phenotypic variation (Fig. 1). These findings support the fact that S_2-progeny selection has increased the frequency of favorable alleles for grain yield.

There were no agronomically meaningful changes between BS13(S)C0 and BS13(S)C6 for root lodging, stalk lodging, pollen shed, and silk emergence. Responses to S_2-progeny selection for plant (0.7 cm cycle^{-1}) and ear (0.8 cm cycle^{-1}) height were significant and similar to those observed for HS selection. The number of ears plant^{-1} remained unchanged with selection.

Significant responses to S_2-progeny selection were observed for all of the ear traits. The mean

number of kernel rows decreased by 0.5 rows and mean ear length increased 0.7 cm. The significant decreases observed for ear diameter (0.1 cm) and kernel depth (0.07 cm) were not agronomically meaningful. Six cycles of S_2-progeny selection significantly increased the average 300-kernel weight by 1.2 g.

Reciprocal Recurrent Selection

Eleven cycles of RRS significantly improved the mean grain yield in BSSS (Table 1). The average indirect response to selection was 0.77 Mg ha^{-1} or 1.4% cycle^{-1}. This result is similar to the response of 1.2 % cycle^{-1} observed after four cycles of selection by HALLAUER (1971), but it is significantly lower than the response of 2.6 % cycle^{-1} observed by HOLTHAUS and LAMKEY (1995). As was suggested for the HS selection program, differences among studies in the average linear rate of response to RRS may be a function of the number of environments in which the materials were evaluated and/or differences in methods of evaluation and data collection. A mean grain yield increase of approximately one phenotypic standard deviation was accompanied by a reduction in the range of the distribution of more than three phenotypic standard deviations (Fig. 1). Symmetry of the distribution was maintained, but extreme phenotypes were eliminated with selection.

The agronomic traits under secondary selection pressure also responded favorably to RRS. Highly significant decreases in pollen shed and silk emergence (24 and 38 GDU °C, respectively) indicated a trend toward earlier maturity in BSSS. A slight decrease in the percentage of root lodged plants (1.9%) and a significant decrease in the percentage of stalk lodged plants (5.4%) were also observed. HALLAUER (1971) reported similar responses for silk date and root and stalk lodging. Responses to RRS for the plant and ear traits were generally favorable. The average plant and ear height significantly decreased 0.8 and 1.9 cm cycle^{-1}, respectively. The relatively large increase in the mean number of ears plant^{-1} (0.14) was not significant because of a large genotype x year interaction. The mean kernel row number increased significantly and ear length decreased slightly with selection. Ear diameter, kernel depth, and 300-kernel weight did not change with selection. After four cycles of RRS, HALLAUER (1971) observed similar responses for plant and ear height, ear length and diameter, and kernel depth in the BSSS population per se.

Effects of Selection on Genetic Variance

For most traits, the within-population mean squares for males, females, males and females pooled, males x females, and their appropriate interaction with years were generally significant or highly significant. The interactions with years, however, were generally much smaller than the main effects. The within-population sources of variation indicate that significant genetic variation among the half-sib and full-sib progenies was present in each population for all traits.

Half-sib Progeny Selection

All variance components for grain yield in BSSSC0 and BS13(S)C0 were significant except for the additive x year interaction in BSSSC0 (Table 2). Additive and dominance variance contributed equally to the total genetic variation in BSSSC0. This result is consistent with the results of HALLAUER (1971) and HOLTHAUS and LAMKEY (1995). No significant changes in variance components were observed after seven cycles of HS progeny selection. Additive genetic variance and dominance x year interaction variance, however, were reduced by 55 and 62%, respectively. The additive x year interaction increased by 226%, but the confidence intervals were too wide to declare the difference significant. The changes in the genetic variance components for grain yield were similar to those reported by STUCKER and HALLAUER (1992) and consistent with those reported by HOLTHAUS and LAMKEY (1995).

Additive genetic variance was significantly different from zero in BSSSC0 and BS13(S)C0 for all traits except root lodging in BSSSC0. There was a significant difference for additive genetic variance between BSSSC0 and BS13(S)C0 for kernel row number, but differences for all other traits were nonsignificant. Additive variance accounted for most of the total genetic variance for pollen shed, plant height, ear height, kernel row number, ear diameter, and 300-kernel weight.

Dominance genetic variance was significantly greater than zero for pollen shed, silk emergence, ear height, kernel row number, ear length, and 300-kernel weight in BSSSC0 and root lodging, silk emergence, and ear length in BS13(S)C0. With the exception of root and stalk lodging, the general trend was for dominance variance to decrease with selection. There was a significant reduction in dominance variance after HS selection for pollen shed, silk emergence, ear height, and kernel row number.

Our results are generally consistent with the results of HALLAUER (1971), STUCKER and HALLAUER (1992), and HOLTHAUS and LAMKEY (1995). HOLTHAUS and LAMKEY (1995) reported a significant increase in

TABLE 2 - *Estimates of genetic components of variance, their interactions with years, and the ratio of additive and dominance variances from the combined analyses of variance over 1992 and 1993 for 13 traits in four BSSS populations.*

Trait	Genetic components of variance†				
	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_D$	$\hat{\sigma}^2_{AY}$	$\hat{\sigma}^2_{DY}$	$\hat{\sigma}^2_D / \hat{\sigma}^2_A$
Grain yield (Mg ha^{-1})					
BSSSC0	0.443	0.469	0.084	0.472	1.06
	(0.214,0.763)‡	(0.132,0.859)	(−0.081,0.277)	(0.113,0.946)	
BS13(S)C0	0.200	0.336	0.274	0.179	1.68
	(0.052,0.394)	(0.165,0.540)	(0.159,0.435)	(0.010,0.398)	
BS13(S)C6	0.363	0.254	0.379	0.143	0.70
	(0.171,0.623)	(0.088,0.446)	(0.239,0.578)	(−0.039,0.376)	
BSSS(R)C11	0.366	0.073	0.068	0.146	0.20
	(0.244,0.546)	(−0.04,0.197)	(0.000,0.153)	(0.003,0.330)	
Root lodging (%)					
BSSSC0	2.16	2.65	16.95	−8.05	1.23
	(−4.08,9.25)	(−4.30,9.91)	(10.26,26.43)	(−18.12,4.05)	
BS13(S)C0	20.16	21.70	8.18	2.83	1.08
	(7.95,36.64)	(2.71,42.92)	(−1.82,20.38)	(−20.42,31.65)	
BS13(S)C6	10.51	3.04	9.81	34.89	0.29
	(−1.08,24.85)	(−18.37,24.77)	(−2.93,25.26)	(7.14,70.80)	
BSSS(R)C11	−0.20	−0.47	1.00	0.56	2.31
	(−1.25,0.92)	(−2.72,1.72)	(−0.39,2.67)	(−2.66,4.59)	
Stalk lodging (%)					
BSSSC0	37.39	9.14	−1.62	5.80	0.25
	(22.44,59.15)	(−13.15,32.49)	(−13.06,10.76)	(−23.77,43.10)	
BS13(S)C0	17.03	14.98	17.08	−3.96	0.88
	(4.62,33.22)	(−2.31,33.82)	(6.01,31.52)	(−26.51,23.63)	
BS13(S)C6	20.30	13.05	7.12	−0.46	0.64
	(9.37,35.26)	(−3.36,30.80)	(−1.91,18.10)	(−21.81,25.82)	
BSSS(R)C11	9.21	6.43	4.11	−15.71	0.70
	(2.67,17.83)	(−4.72,18.26)	(−2.10,11.56)	(−31.85,3.35)	
Pollen shed (GDU °C)					
BSSSC0	321.8	185.0	23.4	18.1	0.58
	(226.5,466.2)	(120.1,269.8)	(−1.0,53.5)	(−34.0,84.2)	
BS13(S)C0	251.1	32.0	9.4	18.0	0.13
	(184.7,352.1)	(−10.2,77.6)	(−12.5,35.1)	(−35.9,85.2)	
BS13(S)C6	221.3	61.9	23.5	−12.0	0.28
	(160.7,312.8)	(27.8,102.2)	(5.8,46.1)	(−50.5,34.7)	
BSSS(R)C11	343.4	29.2	31.5	28.2	0.09
	(255.7,477.1)	(−7.0,68.5)	(8.8,60.6)	(−16.5,85.0)	
Silk emergence (GDU °C)					
BSSSC0	274.4	278.9	36.1	−28.1	1.02
	(177.5,418.1)	(188.7,398.4)	(4.0,76.5)	(−98.5,58.5)	
BS13(S)C0	216.4	70.2	28.7	17.0	0.33
	(151.1,314.2)	(19.2,128.5)	(1.5,62.6)	(−42.6,91.3)	
BS13(S)C6	232.9	104.6	32.2	10.0	0.45
	(162.8,337.8)	(53.1,166.6)	(6.8,64.4)	(−43.6,76.6)	
BSSS(R)C11	485.3	23.7	44.2	60.1	0.05
	(359.8,676.9)	(−36.3,86.3)	(6.4,91.8)	(−17.4,159.1)	
Plant height (cm)					
BSSSC0	77.4	11.9	−6.0	19.2	0.15
	(56.6,109.5)	(−4.9,30.0)	(−13.7,1.6)	(−1.1,45.6)	
BS13(S)C0	73.2	8.5	3.4	5.0	0.12
	(53.3,103.5)	(−5.6,23.5)	(−4.1,12.2)	(−13.4,27.9)	

TABLE 2 - *Continued.*

Trait	Genetic components of variance[1]				
	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_D$	$\hat{\sigma}^2_{AY}$	$\hat{\sigma}^2_{DY}$	$\hat{\sigma}^2_D / \hat{\sigma}^2_A$
BS13(S)C6	103.9	2.0	5.2	13.1	0.02
	(77.9,143.6)	(–10.5,14.7)	(–2.1,14.1)	(–3.5,34.2)	
BSSS(R)C11	74.6	6.0	10.6	–3.3	0.08
	(53.9,105.9)	(–6.1,18.7)	(2.8,20.7)	(–19.8,16.9)	
Ear height (cm)					
BSSSC0	70.2	34.2	6.8	10.3	0.49
	(48.1,103.5)	(16.0,56.2)	(–1.7,17.1)	(–8.2,34.0)	
BS13(S)C0	78.7	3.7	5.0	18.0	0.05
	(58.3,109.8)	(–7.7,15.4)	(–1.6,13.0)	(3.6,36.6)	
BS13(S)C6	102.6	5.6	0.9	13.9	0.06
	(77.4,141.1)	(–6.4,18.3)	(–5.4,7.9)	(–1.4,33.6)	
BSSS(R)C11	97.1	16.2	10.7	–5.8	0.17
	(71.2,136.4)	(3.5,30.5)	(3.2,20.4)	(–21.5,13.3)	
Ears plant^{-1} (no.)					
BSSSC0	0.004	0.004	0.005	0.003	0.99
	(0.001,0.008)	(0.000,0.009)	(0.002,0.009)	(–0.002,0.009)	
BS13(S)C0	0.004	0.003	0.001	0.002	0.65
	(0.002,0.007)	(–0.001,0.007)	(–0.001,0.004)	(–0.003,0.009)	
BS13(S)C6	0.006	0.000	0.005	0.006	0.07
	(0.002,0.010)	(–0.004,0.004)	(0.002,0.009)	(0.000,0.012)	
BSSS(R)C11	0.001	0.002	0.001	0.002	1.54
	(0.000,0.003)	(0.000,0.004)	(0.000,0.003)	(0.000,0.005)	
Kernel row number (no.)					
BSSSC0	2.27	0.47	0.12	–0.14	0.21
	(1.69,3.16)	(0.25,0.73)	(0.02,0.25)	(–0.37,0.12)	
BS13(S)C0	1.11	0.09	0.04	–0.01	0.08
	(0.83,1.54)	(–0.06,0.25)	(–0.04,0.14)	(–0.21,0.24)	
BS13(S)C6	0.87	0.06	0.01	0.01	0.07
	(0.66,1.21)	(–0.04,0.17)	(–0.04,0.08)	(–0.13,0.18)	
BSSS(R)C11	1.50	0.10	0.11	0.04	0.07
	(1.12,2.07)	(–0.05,0.26)	(0.02,0.22)	(–0.15,0.28)	
Ear length (cm)					
BSSSC0	0.659	0.803	0.205	–0.160	1.22
	(0.356,1.092)	(0.442,1.253)	(0.035,0.419)	(–0.527,0.289)	
BS13(S)C0	0.634	0.400	0.344	–0.286	0.63
	(0.363,1.017)	(0.139,0.701)	(0.173,0.575)	(–0.611,0.099)	
BS13(S)C6	0.791	0.278	0.321	–0.063	0.35
	(0.511,1.199)	(0.062,0.522)	(0.169,0.529)	(–0.328,0.261)	
BSSS(R)C11	0.901	0.255	0.102	0.047	0.28
	(0.636,1.301)	(0.058,0.479)	(–0.003,0.232)	(–0.186,0.338)	
Ear diameter (cm)					
BSSSC0	0.027	0.008	–0.001	0.010	0.31
	(0.016,0.043)	(–0.007,0.025)	(–0.009,0.007)	(–0.010,0.036)	
BS13(S)C0	0.035	–0.002	–0.011	0.039	–0.05
	(0.019,0.056)	(–0.033,0.029)	(–0.026,0.005)	(–0.002,0.092)	
BS13(S)C6	0.032	0.004	–0.010	–0.003	0.13
	(0.016,0.053)	(–0.027,0.035)	(–0.025,0.005)	(–0.046,0.051)	
BSSS(R)C11	0.024	0.000	0.001	0.007	0.02
	(0.018,0.034)	(–0.004,0.005)	(–0.001,0.004)	(0.002,0.014)	

TABLE 2 - *Continued.*

Trait	Genetic components of variance†				
	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_D$	$\hat{\sigma}^2_{AY}$	$\hat{\sigma}^2_{DY}$	$\hat{\sigma}^2_D / \hat{\sigma}^2_A$
Kernel depth (cm)					
BSSSC0	0.004	0.000	0.001	0.000	0.11
	(0.002,0.007)	(−0.003,0.004)	(−0.001,0.003)	(−0.004,0.005)	
BS13(S)C0	0.007	−0.004	−0.005	0.012	−0.61
	(0.004,0.011)	(−0.012,0.003)	(−0.008,−0.001)	(0.001,0.025)	
BS13(S)C6	0.004	0.002	−0.003	−0.002	0.41
	(0.001,0.008)	(−0.006,0.010)	(−0.007,0.000)	(−0.013,0.012)	
BSSS(R)C11	0.003	0.001	0.001	−0.001	0.19
	(0.002,0.004)	(−0.001,0.002)	(0.000,0.002)	(−0.003,0.001)	
300-kernel weight (g)					
BSSSC0	36.56	15.19	10.43	−7.00	0.42
	(23.88,55.37)	(5.02,27.08)	(4.20,18.68)	(−19.19,7.84)	
BS13(S)C0	28.44	6.36	16.15	11.60	0.22
	(15.93,45.92)	(−6.64,20.02)	(6.93,28.39)	(−5.13,32.82)	
BS13(S)C6	22.37	18.92	9.38	16.47	0.85
	(12.39,36.46)	(7.50,32.26)	(3.04,17.61)	(4.62,31.86)	
BSSS(R)C11	28.19	−4.39	1.89	15.74	−0.16
	(19.90,40.68)	(−12.39,3.15)	(−2.92,7.49)	(4.78,30.07)	

† $\hat{\sigma}^2_A$, $\hat{\sigma}^2_D$, $\hat{\sigma}^2_{AY}$, and $\hat{\sigma}^2_{DY}$ the additive, dominance, additive x year interaction, and dominance x year interaction components of variance, respectively.

‡ Values in parentheses are the approximate upper and lower 90% confidence interval bounds, respectively, for the variance components calculated according to the procedures of BURDICK and GRAYBILL (1992).

the additive, additive x environment, and dominance x environment variance components for root lodging and a significant decrease in the dominance and additive x environment variance components for stalk lodging after HS selection. STUCKER and HALLAUER (1992) reported a decrease in the dominance variance for days to anthesis, ear length, and ear diameter and a decrease in additive variance for ear length.

S_2 Progeny Selection

All variance components for grain yield in BS13(S)C6 were significantly different from zero, except for the dominance x year interaction estimate. The additive and dominance variances were similar in magnitude. There were no significant changes in any of the variance components for grain yield after six cycles of S_2-progeny selection, although additive and additive x year interaction components increased 82 and 38%, respectively. HOLTHAUS and LAMKEY (1995) also reported that there were no significant differences in variance components between BS13(S)C0 and BS13(S)C6, although the dominance variance increased 51%.

The additive genetic variance was significantly different from zero for all traits except root lodging in BS13(S)C6. The were no significant differences between BS13(S)C6 and BS13(S)C0 for additive genetic variance. Most of the genetic variance for pollen shed, silk emergence, plant height, ear height, ears plant^{-1}, kernel row number, ear length, ear diameter, and kernel depth was additive variance.

Dominance variance was significantly different from zero in BS13(S)C6 for pollen shed, silk emergence, ear length, and 300-kernel weight. There were no significant changes in dominance variance after S_2-progeny selection.

Reciprocal Recurrent Selection

All variance components for grain yield were significantly different from zero in BSSS(R)C11, except dominance variance and the additive x year interaction variance. All variance components for grain yield were reduced after 11 cycles of RRS, although none of the differences was significant. Most of the total genetic variance for grain yield in the population per se after RRS consisted of additive variance. HALLAUER (1971) found similar trends after four cycles of selection and HOLTHAUS and LAMKEY (1995) report-

TABLE 3 - *Heritability estimates (h2) on a half-sib progeny mean basis from the combined analysis of variance over 1992 and 1993 for 13 traits measured in four BSSS populations.*

Trait	$\hat{h}2$	90% confidence interval † Lower	Upper
Grain yield			
BSSSC0	0.538	0.302	0.691
BS13(S)C0	0.383	0.121	0.571
BS13(S)C6	0.502	0.285	0.655
BSSS(R)C11	0.727	0.585	0.818
Root lodging			
BSSSC0	0.131	–0.295	0.414
BS13(S)C0	0.472	0.211	0.644
BS13(S)C6	0.320	–0.069	0.554
BSSS(R)C11	–0.103	–0.786	0.291
Stalk lodging			
BSSSC0	0.674	0.459	0.794
BS13(S)C0	0.409	0.123	0.599
BS13(S)C6	0.521	0.273	0.680
BSSS(R)C11	0.436	0.128	0.627
Pollen shed			
BSSSC0	0.783	0.688	0.850
BS13(S)C0	0.853	0.773	0.903
BS13(S)C6	0.822	0.742	0.877
BSSS(R)C11	0.875	0.81	0.916
Silk emergence			
BSSSC0	0.682	0.545	0.779
BS13(S)C0	0.767	0.567	0.841
BS13(S)C6	0.763	0.658	0.836
BSSS(R)C11	0.869	0.799	0.913
Plant height			
BSSSC0	0.865	0.771	0.916
BS13(S)C0	0.837	0.747	0.892
BS13(S)C6	0.890	0.827	0.928
BSSS(R)C11	0.825	0.735	0.883
Ear height			
BSSSC0	0.754	0.637	0.833
BS13(S)C0	0.867	0.793	0.912
BS13(S)C6	0.904	0.847	0.938
BSSS(R)C11	0.844	0.771	0.894
Ears plant^{-1}			
BSSSC0	0.389	0.094	0.587
BS13(S)C0	0.492	0.215	0.664
BS13(S)C6	0.494	0.232	0.661
BSSS(R)C11	0.304	–0.056	0.534
Kernel row number			
BSSSC0	0.884	0.832	0.921
BS13(S)C0	0.877	0.809	0.919
BS13(S)C6	0.897	0.838	0.932
BSSS(R)C11	0.891	0.835	0.927
Ear length			
BSSSC0	0.566	0.370	0.702
BS13(S)C0	0.591	0.409	0.717
BS13(S)C6	0.679	0.534	0.779
BSSS(R)C11	0.785	0.681	0.854
Ear diameter			
BSSSC0	0.676	0.468	0.794
BS13(S)C0	0.649	0.359	0.789
BS13(S)C6	0.612	0.317	0.762
BSSS(R)C11	0.865	0.782	0.913
Kernel depth			
BSSSC0	0.555	0.284	0.713
BS13(S)C0	0.715	0.282	0.852
BS13(S)C6	0.456	0.020	0.670
BSSS(R)C11	0.649	0.458	0.768
300-kernel weight			
BSSSC0	0.701	0.562	0.797
BS13(S)C0	0.594	0.394	0.726
BS13(S)C6	0.574	0.382	0.707
BSSS(R)C11	0.813	0.678	0.883

† Exact 90% confidence intervals were calculated according to the procedures of KNAPP and BRIDGES (1987).

ed significant decreases in the dominance variance and dominance x environment interaction variance.

Additive genetic variance was significantly different from zero for all traits except root lodging in BSSS(R)C11. There were no significant differences for additive genetic variance between BSSSC0 and BSSS(R)C11 for any trait, except stalk lodging. HALTHAUS and LAMKEY (1995) reported significant decreases in additive genetic variance for root lodging and stalk lodging. The lack of a significant change in root lodging in our study is likely due to poor expression of root lodging in our limited sample of environments. Additive genetic variance was the primary component of total genetic variance for all traits except root lodging, stalk lodging, and ears plant^{-1}.

Dominance genetic variance was significantly dif-

TABLE 4 - *Phenotypic (above diagonal) and additive genetic (below diagonal) correlations among 13 traits based on half-sib progenies in four BSSS populations.*

Trait	Population	Grain yield	Root lodging	Stalk lodging	Pollen shed	Silk emergence	Plant height	Ear height	Ears plant-1	Kernel row number	Ear length	Ear diameter	Kernel depth	300-kernel weight
Grain yield	BSSSC0		0.04	0.29*	–0.01	–0.19	0.25	0.27*	0.65**	–0.15	0.49**	0.17	0.14	0.23
	BS13(S)C0		0.41**	0.24	0.24	0.16	0.43**	0.41**	0.33*	–0.07	0.25	0.17	0.25	0.19
	BS13(S)C6		0.26	–0.04	0.23	0.15	0.37**	0.31*	0.59**	0.05	0.44**	0.39**	0.37**	0.46**
	BSSS(R)C11		–0.04	0.09	0.31*	0.20	0.36**	0.38**	0.36**	–0.18	0.28*	0.24	0.22	0.47**
Root lodging	BSSSC0	–0.11		0.01	0.06	0.01	0.18	0.17	–0.05	–0.10	0.23	–0.09	0.03	0.21
	BS13(S)C0	0.95		0.00	0.18	0.16	0.42	0.47**	0.27*	0.12	0.02	0.26	0.26	0.09
	BS13(S)C6	0.85		0.00	0.25	0.20	0.38**	0.26	0.23	–0.04	0.26	0.12	0.13	0.15
	BSSS(R)C11	–0.20		0.23	0.12	0.02	0.16	0.25	0.00	0.12	–0.20	0.19	0.18	0.09
Stalk lodging	BSSSC0	0.32	0.01		–0.07	–0.13	0.32*	0.33*	0.19	0.09	0.26	0.17	0.10	0.00
	BS13(S)C0	0.03	0.12		–0.28*	–0.30*	0.02	0.09	–0.03	–0.13	–0.17	0.05	0.09	–0.07
	BS13(S)C6	0.25	0.05		0.09	0.00	–0.06	0.16	0.18	–0.02	–0.08	–0.16	–0.16	–0.17
	BSSS(R)C11	–0.06	0.88		0.01	–0.08	0.09	0.24	0.07	–0.05	0.08	0.18	0.17	0.08
Pollen shed	BSSSC0	–0.09	0.22	–0.02		0.88**	0.27*	0.53**	0.01	0.12	–0.03	0.22	0.17	–0.09
	BS13(S)C0	0.56	0.24	–0.50		0.90**	0.45**	0.43**	0.11	0.22	0.16	0.15	0.09	0.17
	BS13(S)C6	0.39	0.47	0.01		0.90**	0.44**	0.67**	0.39**	0.22	0.23	0.23	0.06	0.07
	BSSS(R)C11	0.39	0.62	–0.09		0.93**	0.54**	0.56**	0.01	–0.05	0.17	0.19	0.11	0.27*
Silk Emergence	BSSSC0	–0.14	–0.20	–0.12	0.92		0.19	0.41**	–0.14	0.21	–0.10	0.21	0.14	–0.11
	BS13(S)C0	0.43	0.29	–0.65	0.96		0.42**	0.31*	0.07	0.27*	0.21	0.08	–0.01	0.08
	BS13(S)C6	0.36	0.46	–0.14	0.93		0.48**	0.56**	0.25	0.23	0.25	0.20	0.02	0.09
	BSSS(R)C11	0.30	0.04	–0.14	0.95		0.51**	0.47**	–0.15	0.03	0.17	0.18	0.05	0.24
Plant height	BSSSC0	0.38	0.42	0.36	0.30	0.19		0.60**	0.25	–0.14	0.51**	0.00	–0.04	0.10
	BS13(S)C0	0.62	0.56	0.04	0.50	0.48		0.81**	–0.09	0.10	0.19	0.34*	0.29*	0.24
	BS13(S)C6	0.45	0.74	–0.16	–0.01	0.58		0.74**	0.24	–0.02	0.17	0.30*	0.29*	0.25
	BSSS(R)C11	0.41	0.84	0.12	0.57	0.58		0.77**	–0.05	–0.05	0.28	0.21	0.03	0.23
Ear height	BSSSC0	0.38	0.43	0.49	0.51	0.40	0.65		0.26	–0.01	0.27*	0.18	0.14	–0.02
	BS13(S)C0	0.65	0.71	0.08	–0.03	–0.02	0.86		0.07	0.00	–0.05	0.39**	0.34*	0.25
	BS13(S)C6	0.43	0.51	0.18	0.69	0.61	0.76		0.44**	0.12	0.16	0.26	0.16	0.07
	BSSS(R)C11	0.42	0.10	0.18	0.58	0.50	0.80		0.10	–0.17	0.13	0.20	0.09	0.31*

TABLE 4 - *Continued.*

Trait	Population	Grain yield	Root lodging	Stalk lodging	Pollen shed	Silk emergence	Plant height	Ear height	Ears plant-1	Kernel row number	Ear length	Ear diameter	Kernel depth	300-kernel weight
Ears plant^{-1}	BSSSC0	0.76	–0.35	0.26	0.08	–0.08	0.38	0.33		–0.31*	0.34*	–0.10	–0.15	–0.05
	BS13(S)C0	0.48	0.70	–0.03	0.21	0.19	–0.12	0.08		–0.34*	0.13	–0.03	–0.05	–0.06
	BS13(S)C6	0.70	0.49	0.53	0.15	0.16	0.21	0.50		–0.04	0.34*	0.17	0.12	–0.03
	BSSS(R)C11	0.36	0.11	–0.27	0.10	–0.15	–0.09	0.07		–0.05	0.00	–0.10	0.07	–0.22
Kernel row number	BSSSC0	–0.21	–0.30	0.15	0.10	0.24	–0.17	–0.03	–0.55		–0.31*	0.56**	0.31*	–0.48**
	BS13(S)C0	–0.11	0.23	–0.25	0.25	0.36	0.09	–0.03	–0.56		0.06	0.16	0.08	–0.39**
	BS13(S)C6	0.05	–0.03	–0.08	0.27	0.27	–0.01	0.15	–0.03		–0.03	0.31*	0.19	–0.35**
	BSSS(R)C11	–0.23	–0.19	–0.15	–0.05	0.03	–0.04	–0.16	–0.08		–0.42**	0.51**	0.39**	–0.31*
Ear length	BSSSC0	0.59	0.71	0.27	0.08	–0.02	0.70	0.42	0.35	–0.41		–0.11	–0.08	0.17
	BS13(S)C0	0.10	–0.01	–0.16	0.25	0.35	0.21	–0.02	0.10	0.11		–0.01	–0.08	–0.02
	BS13(S)C6	0.28	0.73	–0.04	0.34	0.42	0.14	0.16	0.42	–0.04		0.09	–0.03	0.17
	BSSS(R)C11	0.22	–0.58	0.14	0.23	0.24	0.31	0.19	0.03	–0.46		–0.32*	–0.33*	–0.11
Ear diameter	BSSSC0	0.16	–0.61	0.09	0.36	0.42	0.01	0.24	–0.28	0.65	–0.39		0.66**	0.14
	BS13(S)C0	0.04	0.61	0.19	0.18	0.19	0.34	0.44	–0.19	0.15	–0.22		0.90**	0.37**
	BS13(S)C6	0.42	0.36	–0.36	0.27	0.23	0.34	0.29	–0.05	0.40	–0.10		0.89**	0.22
	BSSS(R)C11	0.18	0.67	0.03	0.19	0.21	0.19	0.18	–0.27	0.53	–0.42		0.74**	0.41**
Kernel depth	BSSSC0	0.17	–0.21	0.07	0.31	0.30	–0.08	0.14	–0.46	0.41	–0.09	0.78		0.18
	BS13(S)C0	0.32	0.58	0.29	0.04	–0.02	0.26	0.35	–0.14	0.05	–0.18	0.93		0.31*
	BS13(S)C6	0.56	0.29	–0.43	0.02	–0.09	0.38	0.18	–0.12	0.30	–0.27	0.88		0.25
	BSSS(R)C11	0.16	0.16	0.09	0.09	0.02	–0.04	0.05	–0.08	0.47	–0.56	0.83		0.27*
300-kernel weight	BSSSC0	0.31	0.35	–0.05	–0.03	–0.12	0.16	0.03	–0.07	–0.54	0.14	0.05	0.16	
	BS13(S)C0	0.05	0.04	0.11	0.25	0.18	0.30	0.37	–0.13	–0.57	–0.13	0.55	0.41	
	BS13(S)C6	0.36	0.22	–0.07	0.04	0.08	0.30	0.09	–0.18	–0.45	0.03	0.23	0.35	
	BSSS(R)C11	0.43	0.59	0.02	0.30	0.27	0.21	0.28	–0.47	–0.37	–0.20	0.43	0.29	

*, ** Phenotypic correlations significant at the 0.05 and 0.01 probability levels, respectively.

ferent from zero for ear height and ear length. There was a significant decrease in genetic variance after RRS for pollen shed, silk emergence, and 300-kernel weight. The general trend was for dominance variance to be reduced for all traits after RRS, which is in agreement with KEERATINIJAKAL and LAMKEY's (1993) conclusion that heterozygosity has been reduced in BSSS(R)C11 in comparison with BSSSC0.

Heritability Estimates

Heritability estimates were generally a direct reflection of the importance of additive genetic variance for the trait and population of interest. Heritability was significantly different from zero for all traits except for root lodging in BSSSC0, BS13(S)C6, and BSSS(R)C11 and number of ears plant^{-1} in BSSS(R)C11 (Table 3). Variation among traits for heritability was relatively small and no consistent trends were apparent across traits for individual selection methods. The only significant change in heritability was an increase for silk emergence after 11 cycles of RRS. The heritability estimates were relatively high for pollen shed (83%), silk emergence (77%), plant height (85%), ear height (84%), and kernel row number (89%); intermediate for grain yield (54%), stalk lodging (51%), ear length (66%), ear diameter (70%), kernel depth (59%), and 300-kernel weight (67%); and low for root lodging (21%) and number of ears plant^{-1} (42%). Heritability estimates reported by HOLTHAUS and LAMKEY (1995) for traits that were in common with our study were generally greater because more environments were used for evaluation.

Phenotypic and Additive Genetic Correlations

No consistent changes in phenotypic correlations were apparent across traits for individual selection methods (Table 4). When phenotypic correlations for particular trait combinations are averaged over selection methods, certain trait associations become apparent. Higher grain yield was associated with greater plant and ear height, longer ears, and increased 300-kernel weight. Later pollen shed and silk emergence was associated with greater plant and ear heights, which inherently are highly correlated. More kernel rows per ear were associated with larger diameter ears and lower 300-kernel weights. Larger diameter ears were generally associated with greater kernel depth and increased 300-kernel weight. Genetic correlations generally mirrored phenotypic correlation results with no obvious trends or patterns developing across the three selection methods.

SUMMARY

The results from our study showed that the relative effectiveness of the three selection methods for improving the mean performance for grain yield of the BSSS populations per se ranged from 0.4% cycle^{-1} for HS selection to 1.1% cycle^{-1} for S_2-progeny selection to 1.4% cycle^{-1} for RRS. The magnitude of the linear response to S_2-progeny selection in our study was similar to the results of HOLTHAUS and LAMKEY (1995), but responses for the HS and RRS methods were significantly smaller in our study. Differences among studies in the average linear rate of response may be a function of the number of environments in which the materials were evaluated and/or differences in methods of evaluation and data collection.

There were few significant changes in variance components after selection for most of the traits with all three selection methods. In general, the largest portion of the total genetic variance for all traits consisted of additive variance. Genetic by year interactions were generally unimportant. Our study, however, supports the results of other studies that in BSSS, dominance variance plays a more important role in grain yield than in other maize populations (HALLAUER and MIRANDA, 1988). The large dominance variance in BSSS implies that interpopulation selection methods, such as RRS and testcross selection methods utilizing an inbred tester, may provide greater direct selection responses than intrapopulation selection methods.

The estimates of heritability and corresponding estimates of additive genetic variance indicated that continued response to selection is expected for each selection method. Secondary selection pressure on important agronomic traits, when the primary trait under selection was grain yield, was effective for maintaining or improving their level in the selected populations. Selection pressure on the primary agronomic traits did not seem to affect the mean performance and genetic parameters of other unselected agronomic traits.

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